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STUDIES IN THE CLASSIFICATION AND NOMEN-  
CLATURE OF THE BACTERIA

IX. THE SUBGROUPS AND GENERA OF THE  
THIOBACTERIALES

BY

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*From the Bacteriological Laboratories of the Iowa State College, Ames, Iowa*

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## STUDIES IN THE CLASSIFICATION AND NOMEN- CLATURE OF THE BACTERIA

### IX. THE SUBGROUPS AND GENERA OF THE THIO- BACTERIALES

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#### Order IV. **Thiobacteriales** Ordo nov.

Cells various, typically containing either granules of free sulphur, or bacteriopurpurin, or both, usually growing best in the presence of hydrogen sulphide. The cells are plant-like, not protozoan-like, not producing a pseudoplasmodium or a highly developed encysted resting stage. Spores are rarely or never formed.

Classification within this group is in a very unsatisfactory and very superficial state. Few investigators have studied these forms, and most of the work is old, and in need of careful revision. Undoubtedly many of the genera are to be regarded as growth forms, merely.

The following names have been applied to families, subfamilies, tribes and subtribes.

*Chromatiaceae* Migula, 1900, p. 1047

*Amoebobacterieae* De Toni and Trevisan, 1889, p. 1043

*Beggiatoaceae* Migula, 1895, p. 41

*Amoebobacteriaceae* Migula, 1900, p. 1045

*Thiocapsaceae* Migula, 1900, p. 1042

*Thiopediaceae* Migula, 1900, p. 1044

*Rhodobacteriaceae* Migula, 1900, p. 1042

*Lamprocystaceae* Migula, 1900, p. 1043

*Athiorhodaceae* Molisch, 1907, p. 28

*Thiobacteriaceae* Jensen, 1909, p. 303

*Very few of economic importance*

*Intermediary  
True bacteria  
blue green algae*

The order Thiobacteriales may be divided into families as follows:

*Key to the families of Thiobacteriales*

- A. Cells containing sulphur granules (or in one species possibly oxalate crystals), but no bacteriopurpurin.
  - 1. Unicellular, motile forms. Not filamentous. Family I. *Achromatiaceae*
  - 2. Filamentous forms. Family II. *Beggiatoaceae*
- B. Cells containing bacteriopurpurin with or without sulphur granules. Family III. *Rhodobacteriaceae*

**Family I. Achromatiaceae Fam. nov.**

*Unicellular, large, motile (by means of flagella?) cells containing granules of sulphur (or in one form possibly oxalate), but no bacteriopurpurin.*

The following key will separate the genera recognized.

*Key to the genera of Achromatiaceae*

- A. Cells spherical or ellipsoidal
  - 1. Cells ellipsoidal (spherical when newly divided). Cells containing granules of calcium oxalate (perhaps sulfur). Genus I. *Achromatium*
  - 2. Cells spherical, with sulphur granules in a central vacuole. Genus 2. *Thiophysa*
- B. Cells longer, very large (42 to 86 $\mu$ ) with peritrichous flagella. Genus 3. *Hillhousia*

**Genus 1. Achromatium Schewiakoff 1893**

**Synonyms:**

*Modderula* Frenzel, 1897, p. 901

*Cells large, nearly spherical in newly divided cells to ellipsoidal, 15 to 43 by 9 to 22 $\mu$ . Cells closely packed with large granules, at first interpreted as sulphur, but later interpreted as calcium oxalate. When granules are dissolved, cells show coarse alveolar structure. Cells are motile, flagella not demonstrated. Cell division resembles the constriction of flagellates rather than the fission characteristic of bacteria.*

The type species is *Achromatium oxaliferum* Schewiakoff. The organism occurs in the slime at the bottom of the rivers, in the so called "Modder."



Genus 2. **Thiophysa** Hinze, 1903, p. 310

Spherical cells laden with sulphur. The protoplasmic layer surrounds a large central vacuole. Cell nucleus not recognized. Flagella lacking. Cells elongate before division, divide to biscuit shaped cells. Cells 7 to  $18\mu$  in diameter.

The type species *Thiophysa volutans* Hinze was secured from the Bay of Naples.

Genus 3. **Hillhousia** West and Griffiths, 1909, p. 398

Cells very large, 42 to 86 by 20 to  $33\mu$ . motile by means of peritrichous flagella. Cells packed with large globules of oily amorphous sulphur.

The type species is *Hillhousia mirabilis* West and Griffiths.

Family II. **Beggiatoaceae** Migula, 1895, p. 41

Filamentous bacteria, usually showing an oscillating motion similar to *Oscillatoria*. Cells contain sulphur granules. Spore formation and conidia unknown.

The genera of the family *Beggiatoaceae* may be differentiated by means of the following key:

Key to the genera of *Beggiatoaceae*

A. Filament non-motile, with a contrast to base and tip, attached.

Genus 1. *Thiothrix*

B. Filaments motile (oscillating) not attached, no differentiation into tip and base.

1. Filaments not in bundles nor surrounded by a gelatinous sheath.

Genus 2. *Beggiatoa*

2. Filaments in bundles, surrounded by a gelatinous sheath.

Genus 3. *Thioploca*

Genus 1. **Thiothrix** Winogradsky, 1888, p. 39

Filament non-motile, segmented, a definite differentiation into base and tip, attached, usually filled with sulphur granules. The threads produce rod shaped conidia at their ends. These conidia are self motile by means of a slow creeping motion, attach themselves and develop into new threads. The habitat is hot sulphur springs.

The type species is *Thiothrix nivea*. (Rabenhorst) Winogradsky.

Genus 2. **Beggiatoa** Trevisan, 1842, p. 76

*Threads sheathless, formed of flat discoidal cells, not attached. Multiplication by transverse splitting of the threads. Showing an undulating motion, creeping. Cells contain globules of sulphur. Usually in hot sulphur springs.*

The type species is *Beggiatoa alba* (Vaucher) Trevisan.

Genus 3. **Thioploca** Lauterborn, 1907, p. 238

*Filaments Beggiatoa-like, with numerous sulphur granules, motile, lying parallel in considerable numbers, or united in bundles enclosed in a colorless layer of gelatin.*

The type species, *Thioploca schmidlei* Lauterborn has filaments 5 to 9 $\mu$  thick, and gelatinous sheath 50 to 160 $\mu$  thick. From the ocean bed.

Family III. **Rhodobacteriaceae** Migula, 1900, p. 1042

Synonym:

*Rhodobacteria* Molisch, 1907, p. 27

*Cells of various types, not filamentous, containing bacterio-purpurin with or without sulphur granules also.*

Two subfamilies may be separated by the following key:

*Key to the subfamilies of Rhodobacteriaceae*

- A. Cells containing sulphur granules.....Subfamily I. *Chromatioideae*
- B. Cells without sulphur granules.....Subfamily II. *Rhodobacterioideae*

Subfamily I. **Chromatioideae** Nom. nov.

Synonyms:

*Thiorhodaceae* Molisch, 1907, p. 28

*Cells not filamentous, containing both sulphur granules and bacteriopurpurin.*

The following names have been used for genera in this group:

*Erythroconis* Oersted, 1842, p. 552

*Chromatium* Perty, 1852, p. 179

*Clathrocystis* Henfrey, 1856, p. 53

*Rhabdomonas*, Cohn, 1875, p. 167



- Cohnia* Winter, 1884, p. 48  
*Lamprocystis* Schroeter, 1886, p. 151  
*Lampropedia* Schroeter, 1886, p. 151  
*Mycothece* Hansgirt, 1888, p. 266  
*Amoebobacter* Winogradsky, 1888, p. 71  
*Thiocapsa* Winogradsky, 1888, p. 84  
*Thiocystis* Winogradsky, 1888, p. 60  
*Thiodictyon* Winogradsky, 1888, p. 80  
*Thiopedia* Winogradsky, 1888, p. 85  
*Thiopolycoccus* Winogradsky, 1888, p. 79  
*Thiosarcina* Winogradsky, 1888, p. 104  
*Thiospirillum* Winogradsky, 1888, p. 104  
*Thiothece* Winogradsky, 1888, p. 82  
*Cenomesia* De Toni and Trevisan, 1889, p. 1039  
*Thiosphaerion* Miyoshi, 1897, p. 170  
*Thiosphaera* Miyoshi, 1897, p. 170  
*Rhodocapsa* Molisch, 1906, p. 223  
*Rhodothece* Molisch, 1906, p. 223  
*Amoebomonas* Jensen, 1909, p. 338  
*Thioderma* Miyoshi, 1897, p. 170  
*Rhabdochromatium* Winogradsky, 1888, p. 100

Of these names *Clathrocystis* and *Erythroconis* are algal genera to which certain of the sulphur bacteria have at different times been assigned.

Following is a key to the tribes of the *Chromatioideae* which may be recognized largely from the descriptions of Winogradsky.

*Key to the tribes of Chromatioideae*

- A. Cells united, at least during a part of the life history, into families.
  - I. Cell division such that masses of cells, not merely plates, are formed.
    - a. Cell division in three directions of space.....Tribe I. *Thiocapseeae*
    - b. Cell division first in three, then in two directions of space.
      - Tribe II. *Lamprocysteeae*
  - II. Cell division in two planes, forming plates of cells.
    - Tribe III. *Thiopediaceae*
  - III. Cell division in one plane.....Tribe IV. *Amoebobacteriaceae*
- B. Cells free, capable of swarming at any time.....Tribe V. *Chromatiaceae*

Tribe I. **Thiocapsee** Trib. nov.

## Synonyms:

*Thiocapsaceae* Migula, 1900, p. 1042

*Bacteria containing both sulphur granules and bacteriopurpurin.*  
*Cells divide in three directions of space, united into families.*

*Key to the genera of the Thiocapsee*

## A. Cells capable of swarming.

I. Families small, compact, enclosed singly or several together in a cyst.....Genus I. *Thiocystis*

II. Cells large, 7 to 8 $\mu$  loosely bound by gelatin into loose families  
 Genus II. *Thiosphaera*

III. Cells small, united into solid, spherical families.  
 Genus III. *Thiosphaerion*

## B. Cells not capable of swarming.

I. Spherical cells spread out upon the substratum in flat families, loosely enveloped in a common gelatin.....Genus IV. *Thiocapsa*

II. Arranged in regular packets like *Sarcina*.....Genus V. *Thiosarcina*

Genus I. **Thiocystis** Winogradsky, 1888, p. 60

*Usually 4 to 20 or 30 cells massed into small, compact families, enveloped singly or several together in a gelatinous cyst, capable of swarming. When the families have reached a definite size they escape from the gelatinous cyst, the latter either swelling and softening uniformly or at some particular spot. The escaped cells either pass into the swarm stage or unite into a larger fused complex of families. Cells are light colored, single cells almost colorless. In masses the cells show a beautiful violet or red violet color. The cells are frequently quite filled with sulphur granules.*

The type species is *Thiocystis violacea* Winogradsky.

Genus II. **Thiosphaera** Miyoshi, 1897, p. 170

*Cells spherical-ellipsoidal, relatively large (7 to 8 $\mu$ ) light violet in color, bound into loose families by a colorless gelatin. Capable of swarming. Sulphur inclusions relatively abundant.*

The type species is *Thiosphaera gelatinosa* Miyoshi.



Genus III. **Thiosphaerion** Miyoshi, 1897, p. 170

Cells spherical-ellipsoidal, small (1.8 to 2.5 $\mu$  violet in color, with delicate sulphur inclusions. United by means of gelatin into solid spherical families. Capable of swarming.

The type species is *Thiosphaerion violaceum* Miyoshi.

Genus IV. **Thiocapsa** Winogradsky, 1888, p. 84

Cell families resembling in grouping and multiplication the cells of the algal genus *Aphanocapsa*. Cell division occurs in all directions of space, the cells are spherical, with thick confluent membranes, which unite to form a structureless, gelatinous layer. The cells are of a bright rose red color and contain numerous sulphur granules. The cells do not swarm.

The type species is *Thiocapsa roseo-persicina* Winogradsky.

Genus V. **Thiosarcina** Winogradsky, 1888, p. 104

Synonym:

*Rhodosarcina* Jensen, 1909, p. 334

Non-swarming cells arranged in packet shaped families, corresponding to the genus *Sarcina*. Cells red, with sulphur granules.

The type species is *Thiosarcina rosea* (Schroeter) Winogradsky.

Tribe II. **Lamprocysteae** Trib. nov.

Synonyms:

*Lamprocystaceae* Migula, 1900, p. 1043

Cells united into families in which division of the cells occur first in three planes, then in two.

The single genus of this tribe is *Lamprocystis*.

Genus I. **Lamprocystis** Schroeter, 1886, p. 151

Synonyms:

*Clathrocystis* Cohn, 1875

not *Clathrocystis* Henfrey, 1856, p. 53

*Cohnia* Winter, 1884, p. 48

not *Cohnia* Kunth 1850

not *Cohnia* Reichenbach 1852

*Cenomesia*? De Toni and Trevisan, 1889, p. 1039

Cells ellipsoidal, dividing at first in three planes to form spherical cell masses, later in two planes, forming hollow sacks in which the cells lie embedded in a layer in the walls, finally the membrane ruptures, and the whole mass becomes net like, much as in the algal genus *Clathrocystis*. Usually colored intensely violet. Small sulphur granules present. Capable of swarming.

The type species is *Lamprocystis roseo-persicina* (Cohn) Schroeter.

### Tribe III. Thiopedieae Trib. nov.

#### Synonyms:

*Thiopediaceae* Migula, 1900, p. 1044

Sulphur bacteria in which the cells are united into families, and cell division is in two directions of space, resulting in the development of plates of cells.

The two genera may be differentiated by the following key:

#### Key to the genera of Thiopedieae

- A. Cells occurring regularly in fours.....Genus I. *Lampropedia*
- B. Cells occurring in a film or membrane, not regularly disposed in tetrads.  
Genus II. *Thioderma*

#### Genus I. *Lampropedia* Schroeter, 1886, p. 151

#### Synonyms:

*Erythroconis*? Oersted, 1842, p. 6

*Thiopedia* Winogradsky, 1888, p. 85

Cells united into tetrads, forming flat tubular masses. Contain sulphur granules and bacteriopurpurin.

The type species is *Lampropedia hyalina* (Kuetzing) Schroeter.

#### Genus II. *Thioderma* Miyoshi, 1897, p. 170

Cells spheroidal, light rose in color, containing small, inconspicuous, sulphur granules. United into thin purplish membrane,

The type species is *Thioderma roseum* Miyoshi.



Tribe IV. **Amoebobacterieae** Trib. nov.

## Synonyms:

*Amoebobacteriaceae* Migula, 1900, p. 1045

*Sulphur bacteria in which the cells are united into families. Cell division occurring only in one direction of space.*

*Key to the genera of Amoebobacterieae*

I. Cells connected by plasma threads, families amoeboid motile.

Genus I. *Amoebobacter*

II. Cells not as I.

A. Cells arranged in a net, united by their ends.... Genus II. *Thiodictyon*

B. Cells not arranged in a net.

1. Capable of swarming. Cells loosely aggregated in gelatin.

Genus III. *Thiothece*

2. Non-motile. Cells closely appressed into a colony.

Genus IV. *Thioplyococcus*Genus I. **Amoebobacter** Winogradsky, 1888, p. 71

*Cells connected by plasma threads. Families amoeboid motile. The cell families slowly change form, the cells drawing together into a heap or spreading out widely, thus bringing about a change in the shape of the whole family. In a resting condition a common gelatin is extruded, the surface becomes a firm membrane.*

The type species is *Amoebobacter roseus* Winogradsky.

Genus II. **Thiodictyon** Winogradsky, 1888, p. 80

## Synonym:

*Rhododictyon* Jensen, 1909, p. 334

*Cells rod-shaped or spindle-shaped, with sharply pointed ends, united into a net. The compact mass of rods finally assumes an appearance like that of Hydrodictyon. Slight violet color.*

The type species is *Thiodictyon elegans* Winogradsky.

Genus III. **Thiothece** Winogradsky, 1888, p. 82

*Cells spherical, in families enclosed in a thick gelatinous cyst. Cells capable of swarming and very loosely embedded in a common gelatin. When the swarm stage supervenes, the cells lie more*

loosely, the gelatin is swollen, and the cells swarm out singly and rather irregularly.

The type species is *Thiothece gelatinosa* Winogradsky.

#### Genus IV. **Thioplycoccus** Winogradsky, 1888, p. 79

Families solid, non-motile, consisting of small cells closely appressed. Multiplication of the colonies by the breaking up of the surface into numerous short shreds and lobes which continue to split up into smaller heaps. Cells red.

The type species is *Thioplycoccus ruber* Winogradsky.

#### Tribe V. **Chromatieae** Trib. nov.

Synonym:

*Chromatiaceae* Migula, 1900, p. 1047

Sulphur bacteria in which the cells are not united into families, but free, and capable of swarming at any time.

The genera of the tribe *Chromatieae* may be differentiated by the following key:

##### *Key to the genera of Chromatieae*

- A. Cells motile by means of polar flagella. Elongated.
  - I. Cells not spiral.
    - a. Cells cylindric.....Genus I. *Chromatium*
    - b. Cells with tendency to spindle shape.....Genus II. *Rhodomonas*
  - II. Cells spiral.....Genus III. *Thiospirillum*
- B. Cells spherical, or little elongate, non motile.
  - I. Cells not encapsulated.....Genus IV. *Rhodocapsa*
  - II. Cells encapsulated in pairs.....Genus V. *Rhodothece*

#### Genus I. **Chromatium** Perty, 1852

Synonym:

*Rhodomonas* Jensen, 1909, p. 334

Cells cylindric-elliptical or relatively thick cylindrical. Cell contents red, containing dark sulphur granules. Cells somewhat variable in shape, straight, more or less bent, short cells ovoid and longer forms more cylindrical. Motile by means of polar flagella.

The type species is *Chromatium okenii* Perty.



Genus II. **Rhabdomonas** Cohn, 1875, p. 167

## Synonyms:

*Mantegazzaea* Trevisan, 1879, p. 137 in part*Rhabdochromatium* Winogradsky, 1888, p. 150

*Differentiated from Chromatium by the elongated rod-shaped or spindle-shaped cells. Cells red, with sulphur granules, polar flagella.*

The type species is *Rhabdomonas rosea* Cohn.

Genus III. **Thiospirillum** Winogradsky, 1888, p. 104

## Synonym:

*Ophidomonas?* Ehrenberg.

*Spiral motile bacteria containing sulphur granules and bacteriopurpurin.*

The type species is *Thiospirillum sanguineum* (Ehrenberg) Winogradsky.

Genus IV. **Rhodocapsa** Molisch, 1906, p. 223

*Cells spherical, free (not united into families) not capable of swarming (non-motile). In mass the organisms are cherry red. Contain sulphur granules.*

The type species is *Rhodocapsa suspensa* Molisch.

Genus V. **Rhodothece** Molisch, 1906, p. 223

*Cells usually spherical and in pairs, each surrounded by a spherical or an ellipsoidal capsule. Non-motile. Cells not united into families. Cells contain bacteriopurpurin and sulphur granules.*

The type species is *Rhodothece pendens* Molisch.

Subfamily II. **Rhodobacterioideae** Subfam. nov.

## Synonym:

*Athiorhodaceae* Molisch, 1907, p. 28

*Cells not filamentous, containing bacteriopurpurin but not granules of sulphur.*

The genera of this subfamily have all been described by Molisch. They may be differentiated by the following key:

*Key to the genera of Rhodobacteroideae*

## I. Cells united into families.

A. Cells rod shaped, many embedded in the same slimy capsule.

Genus I. *Rhodocystis*

B. Cells spherical or short rods.

1. In chains, each chain surrounded by a capsule.

Genus II. *Rhodonostoc*2. Cells free.....Genus III. *Rhodosphaera*

C. Cells free and elongate.

1. Cells not bent.

a. Non-motile.....Genus IV. *Rhodobacterium*b. Motile.....Genus V. *Rhodobacillus*

2. Cells bent or curved.

a. Cells short, comma shaped, with single polar flagellum

Genus VI. *Rhodovibrio*b. Cells spiral, with polar flagella..Genus VII. *Rhodospirillum*Genus I. **Rhodocystis** Molisch, 1907, p. 22*Cells rod-shaped, dividing in only one plane embedded in a common slimy capsule.*The type species is *Rhodocystis gelatinosa* Molisch.Genus II. **Rhodonostoc** Molisch, 1907, p. 23*Cells spherical or short rods, in rosary like chains, and embedded in a common gelatinous capsule.*The type species is *Rhodonostoc capsulatus* MolischGenus III. **Rhodosphaera** gen. nov.

Synonym:

*Rhodococcus* Molisch, 1907, p. 20not *Rhodococcus* Zopf, 1891, p. 28*Cells spherical, non-motile, free not united into families.*The type species is *Rhodosphaera capsulatus* (Molisch) Buchanan.Genus IV. **Rhodobacterium** Molisch, 1907, p. 16*Rod shaped cells, non-motile, not united into families.*The type species is *Rhodobacterium capsulatum* Molisch.



Genus V. **Rhodobacillus** Molisch, 1907, p. 14

*Rod shaped cells, solitary usually, motile.*

The type species is *Rhodobacillus palustris* Molisch.

Genus VI. **Rhodovibrio** Molisch, 1907, p. 21.

*Cells short, comma shaped, free, actively motile by means of a single terminal flagellum.*

The type species is *Rhodovibrio parvus* Molisch.

Genus VII. **Rhodospirillum** Molisch, 1907, p. 24

*Cells spiral, actively motile by means of polar flagella.*

*Rhodospirillum rubrum* (Esmarch) Molisch is the type species.

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